

Table 3. Behavior of *M. coerulatus* males before and after the placement of artificial waterholes. Data are number of 30 min observation periods, characterized by different possible behavior classes on day 1 (pre-treatment), and days 2 and 3 (post-treatment).

Behavior	Day 1	Day 2	Day 3
Flying/Foraging	2	0	3
Guarding hole ^a	1	10	12
Perching	3	3	3
Unseen	21	7	6
Sum	27	20	22

^a Same as Table 2.

and oviposition events, argues that males defending light gap waterholes have generally higher fitness as compared to satellite males.

The rapidity with which females located and oviposited in the artificial waterholes indicates that females also are seeking new potential breeding ground. Fred SaintOurs (pers. com.) indicated that he had previously observed only two copulations during 24 weeks of field study. Male behavior may intensify waterhole limitation among females, as a male often will try to prevent females with whom he has not mated from ovipositing at his waterhole (Finke 2000). Intraspecific interactions are also likely to influence the reproductive success of both sexes in waterholes. *G. gracilis* larvae occupy the same type of waterholes as *M. coerulatus* and prey upon *M. coerulatus* whenever the two species co-occur (Finke 2000). This intense competition, however, seems to be limited to the larval stages. In the two cases where *G. gracilis* were observed ovipositing at the natural waterholes, the male *M. coerulatus* did not move from his perch to challenge the *G. gracilis*, even though he actively defended his hole against conspecifics throughout the day.

The paradox of the persistence of the La Selva *M. coerulatus* population remains. If males without territories must wait until a suitable territory becomes available before reproducing, it is difficult to reconcile the ap-

parently low number of suitable waterholes with a population estimated to include at least 20 individuals that were visiting or occupying two light gaps. Of course, there must be more light gap waterholes at La Selva than we found, but this cannot account for the population of adults in the light gaps we studied unless the proportion of light gaps that contain suitable waterholes is much higher in the light gaps we did not search. It seems more likely that sneaking/understory reproduction accounts for a larger proportion of the *M. coerulatus* population than suspected. This suggests that *M. coerulatus* employs a mixed reproductive strategy in which territoriality is preferred, but the sneaking/understory tactics also allow some reproductive success. More extensive searches for light gap waterholes and further exploration of understory waterholes for *M. coerulatus* larvae would provide information about the relative contributions of alternative reproductive strategies to *M. coerulatus* at La Selva.

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DEPENDENCE OF THE HUMMINGBIRD MITE *PROCTOLAEALAPS KIRMSEI* ON FLOWER PHENOLOGY AND HUMMINGBIRD POLLINATION BEHAVIOR

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Abstract: Hummingbird mites are dependent on host flowers for habitat and food resources and on hummingbirds for dispersal between host flowers. Individuals of the hummingbird mite *Proctolaelaps kirmsei*, must regularly travel between *Hamelia patens* flowers within an inflorescence and among inflorescences. We hypothesized that mite abundance is a combined function of this dispersal within and among inflorescences. If within inflorescence dispersal is more important to mite abundance in a given flower, we would expect greater mite abundance on older inflorescences where mite populations would have had more time to colonize and grow than on younger inflorescences. However, if dispersal between inflorescences is more important, we would expect greater mite abundance on inflorescences with the greatest number of closed flowers because hummingbirds may be more likely visit inflorescences with more of these bright, petal-bearing flowers. In fact, mite abundance on focal mature flowers was positively correlated with both total number of flowers per inflorescence and number of closed flowers per inflorescence. Therefore, increased pollinator visitation rates to these larger inflorescences with more immature flowers likely increases the probability of mite colonization to these inflorescences. To maintain this pattern, mite colonization rates need to be greater than mite dispersal rates from the inflorescence, indicating that mites may assess resources on an inflorescence, and remain on inflorescences that will offer them more floral resources in the future.

Key Words: dispersal, *Hamelia patens*, mite, La Selva

INTRODUCTION

In the tropics, many hummingbird-pollinated plants support mite populations. These mites depend on the open flowers of their host plant for habitat and food resources, and on hummingbirds for dispersal between inflorescences. Nearly all of these mite-flower associations are species-specific and it is suggested that host fidelity (obligate or learned) is the result of sexual selection through the improved location of conspecific mates (Colwell 1986). Due to the symbiosis between mites, flowers, and hummingbirds, mite distribution and abundance may be affected greatly by the dynamics of flower phenology and / or hummingbird behavior.

The mite *Proctolaelaps kirmsei* (Gamasina: Ascidae) is a common inhabitant of the hummingbird pollinated *Hamelia patens* (Rubiaceae) flowers (Colwell 1995). *P. kirmsei* depend on open flowers, and due to

the relatively short longevity of individual flowers, individual mites must disperse between flowers within an inflorescence many times during their two week life span. Although most mites spend their entire life on their native inflorescence, the persistence of populations of *P. kirmsei* requires hummingbird-mediated dispersal to colonize new inflorescences. Thus, mite abundance in a given open flower will be a combined function of the within-inflorescence and between-inflorescence dispersal processes, but the relative contributions of these processes to local abundance are unknown.

If within-inflorescence dispersal is more important to mite abundance, we would expect mite abundance to be greatest on older inflorescences where mite populations have had more time to colonize and grow. In contrast, if between-inflorescence dispersal via hummingbirds is more important than within inflorescence dispersal, then we expect mite

abundance to be greatest on inflorescences with the largest number of petal-bearing flowers because hummingbirds are likely to be more attracted to inflorescences that have a greater number of petal-bearing flowers (closed and open).

METHODS

On 17 Feb. 2000 between 09:30 – 10:30, we sampled 26 inflorescences from 14 *Hamelia patens* trees in the laboratory clearing of the La Selva Biological Station, Costa Rica. We haphazardly sampled inflorescences from a wide range of sizes and flower development stages. All inflorescences sampled were < 2 m high, and had at least one open flower. To characterize the age of each inflorescence, we counted the number of closed, open, and senescent flowers (e.g. detached petals or fruits). The mean number of flowers per inflorescence across all developmental stages (± 1 SD) was 21.6 ± 8.7 . We subsequently collected all open flowers on an inflorescence (1–2 flowers), and dissected them to count the number of mites. When an inflorescence supported two open flowers, we calculated the average number of mites per open flower. The mean mite abundance per inflorescence (± 1 SD) was 41.9 ± 68.5 .

To determine the mean age of flowers on an inflorescence, we estimated the number of days an individual flower spends in each developmental stage. We divided the mean number of flowers within each stage by the published turnover rate between stages (1.5 flowers opening and senescing / day; Newstrom et al. 1994), which indicated that an average flower spends 7, 1, and 7 d in the stages we recognized as closed, open, and senescent. It follows then that the average ages of closed, open, and senescent flowers were 3.5, 4.5, and 8 days, respectively. These estimates allowed us to calculate the mean and standard deviation of flower age in each in-

florescence (mean age of all flowers = [(3.5 days • number of closed flowers) + (4.5 days • number of open flowers) + (8 • number of senescent flowers)] / total number of flowers).

To test the general hypothesis that the characteristics of an inflorescence influence mite populations, we analyzed the effect of the total number of flowers per inflorescence, the mean age of flowers within an inflorescence, and standard deviation of flower age within an inflorescence on mite abundance (log transformed) with linear regression models. In addition, we used two separate regression analyses to examine the effect of the abundance of closed and senescent flowers on mite abundance (log transformed).

RESULTS

Mite abundance per open flower was positively correlated with the total number of flowers per inflorescence ($r = 0.37$, $P = 0.06$) and the standard deviation of flower age within an inflorescence ($r = 0.33$, $P = 0.10$), but not the mean age of flowers within an inflorescence (Table 1). More specifically, mite abundance per open flower was positively correlated with the number of closed flowers (Fig. 1), and was not related to the number of senescent flowers ($r = 0.09$, $P = 0.66$, Table 1). None of the possible multiple regression models involving any combinations of these independent variables (total number of flowers per inflorescence, mean age of flowers within an inflorescence, standard deviation of flower age within an inflorescence, number of closed flowers per inflorescence, and number of senescent flowers per inflorescence) provided an appreciably better prediction of mite abundance in an open flower than the simple linear regression in Fig. 1.

DISCUSSION

The positive correlation between mite

Table 1. Correlations between *Proctolaelaps kirmsei* abundance and five measures of flower abundance and age structure of a *Hamelia patens* inflorescence.

	Total number of flowers	Mean age of flowers	Standard deviation of flower age	Number of closed flowers	Number of senescent flowers
Total number of flowers	–	–	–	–	–
Mean age of flowers	0.19	–	–	–	–
Standard deviation of flower age	0.38	0.23	–	–	–
Number of closed flowers	0.59	-0.63	0.21	–	–
Number of senescent flowers	0.68	0.81	0.27	-0.19	–
Mite abundance (log transformed)	0.37	-0.11	0.33	0.40	0.09

abundance and the number of closed flowers per inflorescence suggests that between-inflorescence dispersal has a greater affect on mite abundance than within-inflorescence dispersal. The most probable explanation for this is that hummingbirds are visual foragers, and therefore are more likely to visit *H. patens* inflorescences with abundant and conspicuous petal-bearing flowers (i.e., high numbers of flowers classed as closed and open). This differential visitation may increase the probability that mites colonize and populate inflorescences with more open and total flowers. This hypothesis predicts that hummingbird visita-

tion rates are greater for inflorescences with more petal-bearing flowers.

However, hummingbird preference alone is not sufficient to explain patterns of high mite abundance. If *P. kirmsei* is able to discriminate between different inflorescences based on available and future resources, mites should preferentially colonize inflorescences that provide the best resources and greatest longevity (i.e., number of closed flowers). This predicts that when resources are abundant, mite dispersal rates would be lower than mite colonization rates and that mite dispersal rates would increase in proportion to resource depletion. This could be tested by monitoring mite immigration and emigration across inflorescences with varying amounts of petal-bearing flowers. Based on our explanation, the combination of hummingbird and mite selection of inflorescences should result in a positive correlation between mite abundance and large numbers of petal-bearing flowers (present and future resources) on an inflorescence, and no relationship between mite abundance and the number of senescent flowers (past resources).

In this tightly-woven community, it appears that *P. kirmsei* depends on the relationship between *H. patens* and hummingbird pollinators, and not simply on the flowers or the hummingbirds individually. This multiple-species symbiosis creates an environment where attributes and behavior of one

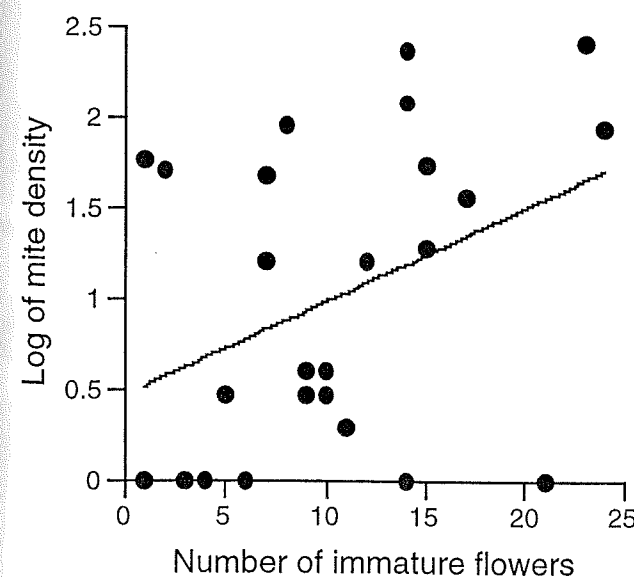


Figure 1. Relationship between number of immature flowers on an inflorescence and mite density (log transformed) per mature flower on the same inflorescence ($n = 26$).

species invariably effect the survival and reproductive fitness of other species in the community. This study demonstrates the complex dynamics that can exist between species in highly specialized coevolutionary relationships.

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